Chapter 3. Diet Overlap, Prey Selection, and Potential Food Competition among Allopatric and Sympatric Forage Fish Species in Prince William Sound, 1996

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Abstract - Chapter 3

We examined forage fish trophic interactions as part of a program studying the abundance, distribution and composition of forage fish populations in Prince William Sound (PWS). Understanding variations in the feeding ecology of these prey of seabirds may help to explain the health of avian predator populations which were impacted during the *Exxon Valdez* Oil Spill.

Juvenile Pacific herring (*Clupea pallasi*), Pacific sandlance (*Ammodytes hexapterus*), and pink salmon (*Oncorhynchus gorbuscha*) occurred sympatrically in 21-41% of the hauls where at least one of the species was present. We examined 467 stomachs of these species collected near shore by beach and purse seine during July, 1996. We also analyzed 50 plankton samples collected concurrently in 20 m vertical hauls with a 0.5 m diameter ring net (243 µm mesh). We compared fish feeding, prey selection from zooplankton, and fish diet overlap in areas with allopatric (single species) and sympatric (multi-species) aggregations.

Zooplankton numerical composition by species was similar at all aggregations (~80% small calanoids). Mean densities ranged from 1800-4200 organisms*m^{-3}. Juvenile herring and sandlance diets were similar (overlap > 60%) only when both were allopatric. Both species consumed small calanoids and larvaceans in proportion to their abundance in the zooplankton, but small calanoids predominated in the diets. Pink salmon diets were not similar to those of either herring or sandlance. Pink salmon selected larvaceans and avoided calanoids. Sandlance were the most adaptable of these planktivores, but pink salmon and herring adhered to similar diets whether allopatric or sympatric.

Changes in diet similarity and declines in prey utilization indicated potential competition among forage species. Diet composition of both herring sympatric with sandlance and sandlance sympatric with herring (n = 4 sets each) shifted significantly (P < 0.05), but not dramatically, from that of herring or sandlance in allopatric aggregations (n = 10 and 14 sets, respectively), providing evidence for partitioning of prey. Sandlance also shifted diets when sympatric with pink salmon. Diet composition of juvenile herring and pink salmon also shifted significantly (P < 0.05) between fish in allopatric (n = 10 and 3 sets, respectively) and sympatric (n = 6, 4 sets, respectively) aggregations, but fish size may have influenced prey composition.

Feeding declines were the most dramatic indication of competition. Measures of food consumption and fullness declined significantly (P < 0.05) for all species in sympatric

aggregations compared to those in allopatric aggregations. Only sandlance sympatric with pink salmon did not feed less. Feeding declines did not appear to be related to fish size or density, but may have been related to decreased zooplankton densities in areas of sympatric aggregations. Our results suggest that competitive interactions limit the feeding of these sympatric forage species, which partially accommodate with shifts in overall diet. The health of forage populations could be affected by such competition if sympatry occurs regularly under conditions of limited food availability.

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Table 1. Sampling region, location, sampling day and time, times at low and high tide, and numbers of fish caught at stations with allopatric and sympatric aggregations of juvenile Pacific herring, Pacific sandlance, and pink salmon in PWS during July, 1996. Samples from stations C and F were collected outside survey sites. Gear abbreviations: BS = beach seine, PS = purse seine, Cast = cast net, Hand = hand dug, P = plankton net. Regions refer to map Figure 1.

Table 2. Mean size and age (A.C.) of fish, preserved fork length (FL) and wet weight, numbers and weights of prey consumed, stomach fullness index, number of empty stomachs (Emp), and prey percent body weight for sets of allopatric and sympatric juvenile Pacific herring, Pacific sandlance and pink salmon at stations in PWS during July, 1996. Ten fish from each station were examined (*indicates exceptions of n = 9). Abbreviations: sem = standard error of the mean.

Table 3. Probability results from 2-way ANOVA on ranks of fish size and measures of total feeding in areas with different species aggregations. The two factors used were "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric\sympatric). Specific paired comparisons were performed when $P < 0.05$ for the interaction terms.

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Table 6. Zooplankton mean density (numbers*m^{-3}) and biomass (mg*m^{-3} wet weight) available to juvenile Pacific herring, Pacific sandlance and pink salmon at stations corresponding to allopatric and sympatric aggregations sampled in PWS during July, 1996. Replicate zooplankton samples were collected in vertical hauls at each station using a 0.5 m diameter ring net with 243 mm mesh. Abbreviations: sem = standard error of the mean.

Table 7a. Zooplankton density (number* m^{-3}) and percent density by taxonomic group and total organisms at areas of allopatric and sympatric aggregations of Pacific herring (H). SL = Pacific Sandlance, PS = Pink Salmon, md = median, sem = standard error of the mean.

Table 7b.   Zooplankton density (number* m^{3}) and percent density by taxonomic group and total at aggregations of allopatric and sympatric pink salmon (PS). H = Herring, SL = Sandlance, md = median, sem = standard error of the mean.

Table 7c.   Zooplankton density (number * m^3) and percent density by taxonomic group and total at aggregations of allopatric and sympatric sandlance (SL). H = Herring, PS = Pink Salmon, md = median, sem = standard error of the mean.

Table 8. Diet similarity (PSI) by percent number and percent biomass of prey species within and between forage species in allopatric and sympatric aggregations in PWS during July, 1996. Diet similarity > 60% is significant.

Table 9.   Probability results from 2-way ANOVA on ranks of prey number and percent number, prey biomass and percent biomass, and prey selection by taxonomic category in areas with different fish species aggregations. The two factors used were "fish species" (Pacific herring, pink salmon and Pacific sandlance) and "aggregation type" (allopatric\sympatric). Specific paired comparisons were performed when the $P < 0.05$ for the interaction terms. Abbreviations: Allo. = Allopatric, Symp. = Sympatric, DNT = Do Not Test.

Table 10a.   Prey utilization and selection for Pacific herring (H). Probability (P) values refer to paired comparisons between allopatric and sympatric aggregations.   Abbreviations: PS = Pink Salmon, SL = Sandlance, md = median, sem = standard error of the mean, DNT = Do Not Test.

Table 10b. Prey utilization and selection for Pink salmon (PS). Probability (P) values refer to comparisons paired between allopatric and sympatric aggregations.   Abbreviations: H = Herring, SL = Sandlance, md = median, sem = standard error of the mean, DNT = Do Not Test.

Table 10c. Prey utilization and selection for Sandlance (SL). Probability (P) values refer to paired comparisons between allopatric and sympatric aggregations.   Abbreviations: H = Herring, PS = Pink Salmon, md = median, sem = standard error of the mean, DNT = Do Not Test.

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Figure 1. Locations of APEX forage fish sampling stations during July, 1996 in PrinceWilliam Sound, Alaska. See also Table 1.

Figure 2. Median fork lengths (FL) of forage fish from sympatric and allopatric aggregations, collected in Prince William Sound during July, 1996. The number of sets (10 fish in each set) is shown below the bars. Results of Mann-Whitney Rank Sum paired comparisons between allopatric and sympatric sizes are indicated: NS = not significant, * $p < 0.05$, *** $p < 0.001$.

Figure 3. Total density (median thousands*m^{-3}) and relative contribution of principal zooplankton taxa available to juvenile Pacific herring, pink salmon, and Pacific sandlance in (a) allopatric and (b) sympatric aggregations in PrinceWilliam Sound during July, 1996.

Figure 4. Diet composition as mean (left side) and median (right side) percent number of prey among allopatric and sympatric aggregations of juvenile forage fish: (a) Pacific herring, (b) pink salmon and © Pacific sandlance collected in Prince William Sound during July, 1996. Legend as in Figure 3. Percentages do not always total 100% due to empty stomachs (see Table 3).

Figure 5. Diet composition as mean (left side) and median (right side) percent biomass of prey among allopatric and sympatric aggregations of juvenile: (a) Pacific herring, (b) pink salmon and © Pacific sandlance collected in Prince William Sound during July, 1996. Legend as in Figure 3. Percentages do not always total 100% due to empty stomachs (see Table 3).

Figure 6. Diet similarity (PSI) by percent number of prey species for forage fish in allopatric and sympatric aggregations collected in Prince William Sound during July, 1996. Line at 60% indicates threshold for significant overlap.

Figure 7. Prey consumption (median prey percent body weight) by forage species in allopatric and sympatric aggregations in Prince William Sound during July, 1996. Results of Mann-Whitney Rank Sum comparisons between groups are indicated: NS = not significant, * $p < 0.05$. See also Table 4.

Figure 8. Feeding selectivity (median Strauss' Linear Selection Index) from principal prey categories among juvenile forage fish: (a) Pacific herring, (b) pink salmon, and © Pacific sandlance. Positive values indicate preference, negative values indicate avoidance. The species composition of allopatric and sympatric aggregations (shown in left-most panels) is repeated across the remaining panels.

Introduction - Chapter 3

The role of forage fish communities is being examined in ecosystems around coastal Alaska and other areas of the world. "Forage fishes are abundant, schooling fishes preyed upon by many species of seabirds, marine mammals, and other fish species. They provide important ecosystem functions by transferring energy from primary or secondary producers to higher trophic levels," (Springer and Speckman, 1997). For example, juvenile Pacific herring (*Clupea pallasi*) and Pacific sandlance (*Ammodytes pacifica*) are forage species with high energy densities that were important to black-legged kittiwakes (*Rissa tridactyla*), while juvenile pink salmon (*Oncorhynchus gorbuscha*)was a low energy density forage species important to tufted puffins (*Fratercula cirhata*; Anthony and Roby, 1997). These and other species have been intensively studied in Prince William Sound (PWS) during damage assessment and ecosystem investigations that ensued with the March, 1989 *Exxon Valdez* (EVOS) oil spill (Brown et. al, 1996). High sea bird mortalities were associated with EVOS and occurred during a period of decline for several sea bird populations in the Gulf of Alaska (Anderson et. al, 1997; Piatt and Anderson 1996). These events were preceded by a two-decade period of shift in the relative abundance of prominent forage fish species (Anderson et al. 1994; Bechtol 1997) and by increased releases of juvenile salmonids into PWS from enhancement facilities. Juveniles of many forage species are abundant and conspicuous during the spring and summer when the breeding and chick- or pup-rearing activities of their avian and mammalian predators are also highly visible. The interplay of environmental conditions, species-specific behaviors, trophic interactions and other factors that influence growth and survival of forage fish and affect the productivity of sea birds are not well understood. However, EVOS studies associated continuing sea bird declines with decreased availability of high quality forage fish prey. Reproductive failures were documented among black-legged kittiwakes from oiled areas (Irons 1996) and may be associated with feeding conditions. Greater declines of pigeon guillemots in oiled areas compared to non-oiled areas were associated with reduced deliveries of Pacific sandlance, a high energy prey, to their chicks (Oakley and Kuletz 1996). Changes in forage fish population could affect their trophic interactions if food availability limits the carrying capacity of PWS (Cooney 1993; Heard 1998).

This diet study is a sub-project of the Alaska Predator Ecosystem Experiment (APEX; Duffy 1997), a multi-disciplinary study designed to understand the PWS food web and its effects on species injured in the *Exxon Valdez* oil spill. Understanding the interactions between forage fish species may help to explain changes in the food habits and reproductive biology of injured marine birds dependent on them, lending support to the APEX hypothesis that "planktivory is the factor determining abundance of the preferred forage species of seabirds." Knowledge about diets, prey availability and selection, shifts in food habits when fish distributions overlap (allopatry vs. sympatry), diel feeding chronology, daily rations and other aspects of feeding ecology, as well as geographic, seasonal, and interannual comparisons of trophic attributes, provides insight into how the population dynamics of forage fish affect the apex predators which use them. Most of what is known about the associations of juvenile Pacific herring, Pacific sandlance and pink salmon relates to them as prey for piscivorous fish, sea birds or marine mammals (Cross et al. 1978; Rogers et al. 1979; Field 1988; Heard 1991; Gilman 1994; Schweigert 1997). Numerous

diet reports have been published, yet the interactions among these species are poorly understood. Especially little is known about Pacific sandlance, principally due to lack of a commercial fishery in the eastern Pacific.

Feeding overlap is one indication of competition. Pacific herring, pink salmon and Pacific sandlance have high potential for feeding overlap due to their shared early life history requirement of nearshore residency (e.g., Simenstad et al. 1979). Competition among species can be inferred from an observed shift in resource use when two species co-occur, such as decreased presence in preferred habitat or decreased use of a preferred prey resource (Sogard 1994). The shift is then reflected in some measure of health, such as poorer condition, less energy reserves, or decreased growth. Ultimately, survival may be affected and populations reduced. For this study, the samples collected for diet studies were adapted to an *a posteriori* experimental design with nine types of species aggregations. We addressed the potential for competition between juvenile Pacific herring, Pacific sandlance and pink salmon by comparing feeding attributes of fish in allopatric aggregations to those in sympatric aggregations with each of the other species. We examined for a) feeding declines, by comparing quantities of food consumed, and for b) diet shifts, by comparing prey composition, prey selection and total diet similarity.

Methods - Chapter 3

The field and laboratory methods used to conduct this study are briefly described herein. Additional details and summaries are described in Duffy (1997).

Field Methods

We sampled schools of forage fish in PWS during July, 1996, using several small-mesh nets deployed from small charter vessels and a 16' skiff, in three regions of the sound (northeast, central, southwest; Figure 1). Samples were collected during offshore and nearshore hydroacoustic surveys conducted concurrently, principally to assess the distribution and abundance of forage species. Offshore hydroacoustic surveys were conducted along parallel transects two miles apart. Offshore fish aggregations detected hydroacoustically were sampled with a midwater research trawl; aggregations detected at the surface were sampled with cast nets and dipnets. The trawl effective mouth opening was 50 m^2, with mesh size diminishing to 9.5 mm in the cod end. A cod end liner with 3.2 mm mesh was added, ending in a plankton cup with 0.5 mm nytex mesh. Nearshore surveys were conducted in each region along zig-zag transects near the beach; a purse seine was used to sample hydroacoustic targets along the 1-km shoreline segment that formed the base of the zig-zag (see Haldorson et al. 1997). The purse seine was 200 m long by 20 m deep, with 25 mm stretched mesh. We also beach seined three randomly selected sections out of the ten comprising each shoreline segment. The beach seine was 37 m long with bridles and lines attached. It tapered from 5 m depth at the center to 1.5 m depth at the ends of each wing. The mesh size was 20 mm stretched, with a center panel of 10 mm mesh.

When fish were caught, duplicate zooplankton samples (20 m vertical hauls, 0.5 m diameter ring net, 243μm mesh) were collected to assess the prey available to fish from pelagic production systems. Zooplankton was collected within 100 m of the beach unless the site was too shallow. Samples were preserved in 5% buffered formaldehyde solution in individual 500 ml bottles. Few plankton samples were collected offshore; therefore, samples collected to complement beach seined fish were paired with fish collected by other nets in the same area (see Table 1).

The object of this study was to address competition of forage fish by comparing their diets when in allopatric and sympatric aggregations. We examined the survey catch data to determine species associations of the catch, defining sympatric as the co-occurrence of two species in a single haul at a station. We classified all sets as allopatric or sympatric according to the following criteria:

Allopatric	Sympatric
● mixed species per area in different hauls	● mixed species in same haul
● 2 species with n < 9 for one of them	● 2 species with n $ 9 each
● 2 size classes of one species (e.g., sandlance, station 11-2B)	● 2 size classes of one species with a co-occurring second species
● additional species present in low numbers, but not of interest (e.g., tomcod)	

Sufficient samples of three species were available (Pacific herring, Pacific sandlance and pink salmon). We analyzed all sympatric sets available, and most of the allopatric sets, including a few non-survey sets. We adapted these samples to an *a posteriori*, experimental design which considered three factors: a) species, b) allopatric vs. sympatric, and c) sympatric species pairing. The design was thus comprised of nine categories of aggregations. Because we pooled sets across regions, the experimental design was not spatially balanced-- all types of aggregations were not captured throughout the sound, even though all three species were present in each region.

Laboratory methods

We examined fish stomach contents to determine: a) if different forage species consumed the same prey types, and b) if feeding shifts occurred between allopatric and sympatric aggregations of any species. Forage fish stomach samples and prey samples (zooplankton) were analyzed at the NMFS Auke Bay Laboratory . Preserved fish were measured and weighed, stomachs were removed and weighed, and indices of stomach fullness and prey digestion were recorded from visual assessment. Relative fullness was recorded as: 1 = empty, 2 = trace, 3 = 25%, 4 = 50%, 5 = 75%, 6 = 100% full, and 7 = distended. The state of digestion was recorded as: 0 = fresh, 1 = partially digested, 2 = mostly digested, 3 = stomach empty. Stomach contents were teased apart and split according to standard subsampling techniques when stomachs were too full to count every prey item (Kask and Sibert 1976). We identified zooplankton to determine selection from pelagic prey fields by fish at each station. Zooplankton samples were split with a

Folsom splitter. Organisms in stomachs and zooplankton samples were identified, enumerated under the microscope, and numbers were expanded. As much as possible, taxa were identified to allow examination of prey selection by species, sex and life history stage, and within size groups. Large copepods were identified as those > 2.5 mm total length (TL). Small copepods were identified as those # 2.5. mm TL, and include the cyclopoid, *Oithona*. Taxa such as euphausiid or amphipod species were similarly defined by length ranges. Prey weight values were taken from data on file at the Auke Bay Laboratory and University of Alaska, Fairbanks, Institute of Marine Science. Prey biomass was calculated by multiplying prey counts by the mean weight per taxon-size class.

Data Summary and Statistical Methods

The abundance and numerical percentage composition of taxa in plankton samples were summarized (means, medians) from pooled stations to characterize the general resources available to planktivores at each station and in the areas of each of the nine types of fish aggregations. The density of planktonic prey was standardized to 1 m³ water volume using the number of animals per sample divided by the volume (V) of water filtered:

$$X = \frac{x_i(1/f)}{V} \quad , \quad V = \pi r^2 D$$

where x_i = number observed per taxon, f = the fraction of the sample analyzed, r = radius of the net (0.25 m) and D = depth of the tow. Depth of plankton samples were generally 20 m, filtering approximately 4 m³ of water.

Ten fish from each species-size group per station were analyzed from diet sample collections. Mean and median preserved fork lengths (FL) of all specimens in each group were calculated to distinguish between intraspecific size/age groups. In general, Pacific herring and sandlance less than 100 mm were considered 0-age and those greater than 100 mm were considered 1-age. All pink salmon were 0-age, but were assigned to two size classes based on similar lengths. Mean and median fullness index and stomach fullness as prey percent body weight (%BW) were also computed:

$$\% \, BW = \frac{\sum (x_i \, w_i)}{BW - (\sum x_i \, w_i)} 100$$

where I = 1 to n prey taxa, x_i = total number of prey per taxon, w_i = the mean weight of each prey taxon in mg, and BW = the fish body weight in mg. Summary fullness indices were then converted back to percentages.

Overall food habits of forage fish species were calculated as means and medians of major

prey categories across all specimens in each fish species aggregation. We present prey biomass, percent total biomass, prey numbers and percent total numbers. Diet similarity was measured at the prey species level on pooled fish using the Schoener Index of Overlap (= Percent Similarity Index, PSI; Wieser, 1960; Schoener 1974; Boesch, 1977; Hurlbert 1978; Krebs 1989):

$$PSI_{jk} = \sum \ \min (p_{ij}, p_{ik}) = 1 - 0.5 * (\sum |p_{ij} - p_{ik}|)$$

where p is the mean numerical or biomass proportion of the ith prey taxon in n taxonomic categories consumed by fish species j and k. The values compared were the means of all fish specimens in the each aggregation type. We calculated three types of diet overlap: interspecific-allopatric fish (two species allopatric), interspecific-sympatric fish (two co-occurring species), and intraspecific allopatric-sympatric fish (an allopatric species compared to itself when sympatric). Values above 60% were considered significant.

Prey selection from zooplankton at the same station was measured for each fish specimen. We used Strauss Linear Selection Index (Ivlev 1961; Krebs 1989; Strauss 1979):

$$L_i = (p_i - e_i) * 100$$

where $I = 1$ to n prey taxa, p_i is the numerical proportion consumed and e_i is the numerical proportion in the prey resource sample. We present mean and median selectivity for all major prey taxa observed in either the stomachs or the plankton for each species aggregation. Negative values indicate avoidance, positive values indicate selection, and values near zero indicate predation at a rate proportional to the abundance of the taxon.

Statistical analyses were based on ten fish observations per station, using stations as replicate observations of the allopatric and sympatric categories. We tested the hypotheses that fish size, fish density (using catch as an index of abundance), total feeding, zooplankton prey availability, and prey utilization and selection did not vary between allopatric and sympatric aggregations depending on the fish species. Two-way analysis of variance (ANOVA) was performed using the factors species (three levels: Pacific herring, pink salmon, and Pacific sandlance) and aggregation type (two levels: allopatric and sympatric). Size included fish FL and wet weight. Total feeding measures included total numbers and biomass of prey consumed, stomach fullness index and prey percent body weight. Measurements of prey availability included density of total zooplankton and density and percent density of major prey categories. We considered prey categories present in the diets or plankton by at least 5% number or weight to be biologically important. All data were tested for normality of distribution and homogeneity of variance. Transformations were usually unsuccessful; therefore, a nonparametric analysis was used. We converted observations to ranks, then applied a two-way ANOVA on the ranked data (Conover 1980). Fish density data were ln-transformed. When the interaction term was significant ($P < 0.05$), specific paired comparisons were performed; for each of the three fish

species, the allopatric values were compared to the two sets of sympatric values (Mann-Whitney Rank Sum Test) to discern differences between aggregation categories. No statistical tests were conducted on measures of diet similarity, which are computed from pooled data. Changes in diet similarity were used to infer prey partitioning and avoidance of competition. We investigated two hypotheses: if competition does not occur, a) two species' diet similarities will be lower when they occur sympatrically compared to when they occur allopatrically, because of prey partitioning; and b) a single species' diet when allopatric will be similar to its diet when sympatric, ie., will not shift.

Results - Chapter 3

Fish diet samples were analyzed from locations in three geographic regions of PWS (Figure 1).   The characteristics of diet sample stations are shown in Table 1 by aggregation type (species x allopatric vs. sympatric with one of the other two species). All samples except one were collected in the second half of July during daylight hours (between 06:35 and 20:15). The frequency of occurrence, abundance and distribution of forage species were summarized elsewhere (Haldorson et al. 1997). In general, forage fish were caught most frequently with beach seines onshore, where fishing effort was focused. They were seldom encountered offshore. Fish were encountered in the northwest more often than in the other regions, with Pacific herring and Pacific sandlance the most frequently-occurring and abundant species. In the central and southwest regions, pink salmon and Pacific tomcod (*Microgadus proximus*) were the most frequently-occurring species. Catches were generally low in the central region, while in the southwest, Pacific herring (mostly adults) were the most abundant species.

Sympatric forage fish aggregations were common on survey transects in July, 1996 (Haldorson et al. 1997). Of the 330 survey hauls that caught fish, juvenile Pacific herring, Pacific sandlance and pink salmon were caught in 39, 22 and 34 sets, respectively. Sympatric species pairs occurred in 21-41% of the hauls catching at least one of these species. All sympatric hauls with sufficient specimens were analyzed (four stations with Pacific herring-Pacific sandlance, four stations with Pacific herring-pink salmon, and one station with Pacific sandlance-pink salmon; Table 1).

The ln-transformed catch by species did not differ between allopatric and sympatric aggregations (2-way ANOVA; interaction term P > 0.05). Most hauls caught < 100 individuals of a species, a few caught several hundred, and 3 sets were in the 10's of thousands (Table 1). Large catches were not restricted to certain aggregation categories. In different hauls, we caught large numbers of Pacific herring sympatric with Pacific sandlance, allopatric sandlance, and sandlance sympatric with herring. For herring and sandlance, the magnitude of the catch differed between the species in three of the four hauls and in both directions. For herring and pink salmon, the magnitude of the catch differed between the species in only one of four hauls.

The mean sizes of both allopatric and sympatric forage fish used for the diet study

indicated that most were 0-age or 1-age (Table 2). Three age classes were indicated for herring. The FLs of specimens used in diet analyses did not vary greatly at any station. Pacific herring mean FL ranged from approximately 30-191 mm. The FLs of herring clustered at # 55 mm, between 100-130 mm, and at 191 mm (one station). Pacific sandlance mean FLs ranged from 61-134 mm per station. The FLs of sandlance clustered in groups of # 89 mm and > 112 mm FL. The FL of pink salmon ranged from 62-130 mm.

We found size differences between allopatric and sympatric fish for all species. The interaction term in a two-way ANOVA testing lengths of forage species in allopatric vs. sympatric aggregations was marginally significant (P = 0.0538; Table 3). Mann Whitney Rank Sum Tests revealed significant differences between median sizes of paired allopatric and sympatric forage fish for each species (Table 4; Figure 2). Herring sympatric with pink salmon were significantly larger (107 mm; P < 0.0001) than allopatric herring (47 mm). However, herring sympatric with sandlance were similar in size (47 mm; P = 0.8280) to allopatric herring. Pink salmon in either type of sympatric aggregation were significantly larger (98 mm; P < 0.0033) than allopatric pink salmon (85 mm). Pacific sandlance sympatric with pink salmon were significantly smaller (64 mm; P < 0.0001) than allopatric sandlance (79 mm), but sandlance sympatric with herring were similar in size (77 mm; P = 0.9287) to allopatric sandlance.

We did not find that certain sizes of a fish species were limited to a single aggregation category. Small and large herring and sandlance specimens were caught at both allopatric stations and at sympatric stations with the other two species (Table 2). Pink salmon were caught less frequently than the others; their full size range was not exhibited across all aggregation types. We did note that some species-size associations were more common than others. Among Pacific herring, the smallest fish were most commonly either allopatric or sympatric with Pacific sandlance. Conversely, the largest herring were most commonly either allopatric or sympatric with pink salmon. Of all sympatric herring, those that co-occurred with sandlance were approximately 50% smaller in FL than the herring that co-occurred with pink salmon (Rank Sum Test, P = 0.0015). Pink salmon sizes varied in sympatric associations with herring. The largest and smallest pink salmon co-occurred with herring, and at two stations, two size classes of pink salmon were present together with herring. Sympatric pink salmon were larger than allopatric individuals, but the two categories of sympatric pink salmon did not differ in FL (P = 0.8866). Among sandlance, the smallest fish were either allopatric or were sympatric with pink salmon, while the largest were either allopatric or were sympatric with herring. The sandlance sympatric with pink salmon were significantly smaller than those sympatric with herring (P < 0.0001).

We found few differences in feeding environment between areas of different fish aggregations. Zooplankton total densities at areas with allopatric and sympatric fish aggregations did not vary with the fish species present (two-way ANOVA on ranks, interaction term P = 0.9611; Table 5). However, densities were marginally significantly higher (2-way ANOVA, species term P = 0.0615; Student-Newman-Keuls all pairwise multiple comparison, P < 0.05) in areas with pink salmon than in areas with sandlance or herring. Mean densities across the nine categories of aggregations ranged from approximately 1800 to 4200*m^{-3} (Table 6).

Zooplankton composition was also similar between allopatric and sympatric aggregations for each species (Figure 3; Table 7a-c). Small copepods comprised at least 72% of the number of zooplankters in the upper 20 m water column. These were principally the calanoids, *Pseudocalanus*, *Acartia*, and *Centropages* and the cyclopoid, *Oithona*. Four taxa comprised the remaining organisms, each < 10%: larvaceans (*Oikopleura dioica*), pteropod gastropods (*Limacina helicina*), cladocerans (*Evadne* sp. and *Podon* sp.), and "other" usually consisting of bivalve larvae. Barnacle larvae and large calanoids (*Calanus pacificus)* were occasionally present (< 3%). The interaction terms from two-way ANOVA's on density and percent density of zooplankton taxa were rarely significant (P > 0.05). Among principal taxa, only the interaction term for percent density of larvaceans was significant (P = 0.0206). Among minor taxa, significant interactions were found only for density and percent density of cladocera (P < 0.0306). Euphausiid larvae density and percent density were marginally significant (P < 0.0545). However, paired comparisons for larvaceans revealed no significant differences (P > 0.05) in composition between areas of allopatric and sympatric aggregations of a species (Table 7).

Diet compositions of forage species in allopatric and sympatric aggregations are presented as percent numbers (Figure 4) and percent biomass (Figure 5) of major prey groups to indicate principal prey and to examine for differences between aggregations. Principal prey differed among forage species, and were: for herring, small calanoids and larvaceans; for pink salmon, larvaceans and fish; and for sandlance, small calanoids. Minor prey included large calanoids, decapod zoeae, barnacle larvae and molts, hyperiid amphipods, cladocera, gammarid amphipods and harpacticoid copepods.

The PSI was used to compare diets between species within aggregation categories and within species between aggregation categories (Figure 6). Among allopatric aggregations, only the diets of sandlance and herring were similar (PSI = 73.1% number; Table 8a). No sympatric species pairs had similar diets (PSI > 60% number or biomass; Table 8b). However, for both pink salmon and herring, diet similarity was high between fish in allopatric and fish in sympatric aggregations (Table 8c). Allopatric sandlance diet was marginally similar (percent biomass) to diet of sandlance sympatric with herring.

Two-way ANOVA'S on the four measures of total feeding produced significant interaction terms (P < 0.0092; Table 3), without exception. This result indicates that, for at least one of the three forage species, measures of total feeding varied according to whether a species occurred allopatrically or sympatrically. Two-way ANOVA's on measures of prey utilization and selection by taxon also yielded significant (P < 0.05) interaction terms, indicating that prey utilization also varied with species composition of the fish aggregation (Table 9). A principal prey, small calanoids, was a notable exception. Although the interaction terms for number and biomass of small calanoids were significant (P < 0.0113), they were only marginally significant (P < 0.0673) for percent number and percent biomass, and were not significant (P = 0.2609) for selection of this taxon. Two-way ANOVA's were followed by paired comparisons within each species.

Herring

Total feeding measures for sympatric herring were significantly lower (Rank Sum Test, P < 0.05) than measures for allopatric herring (Table 4). All four differences were significant for herring sympatric with pink salmon and three out of four were significant for herring sympatric with sandlance. Among all herring, allopatric stomachs were fullest (75%), prey comprised the greatest percent body weight (1.5%), and the median number (383.5 organisms) and biomass (19.97 mg) of prey consumed were greatest. For herring sympatric with pink salmon compared to allopatric herring, significantly lower values included fullness (trace%, P < 0.0001), prey %BW (0.4%, P < 0.0001), total number of prey (24.0, P = 0.0001) and total prey biomass (1.68 mg, P = 0.0035). For herring sympatric with sandlance, values significantly lower than those of allopatric herring included fullness (50%, P = 0.0143), total prey number (269.5, P = 0.0445) and total prey biomass (11.94 mg, P = 0.0158). Only prey %BW was not lower for herring sympatric with sandlance than for allopatric herring (1.1%, P = 0.2546; Figure 7).

The overall diet of allopatric herring was similar to the diet of herring sympatric with pink salmon (Table 8). The PSI was greater than 60% by both number and biomass of prey species. The diet of allopatric herring was also similar to the diet of herring sympatric with sandlance, but only when compared as percent number of prey species. The majority of the prey in common was larvaceans in the first species pairing and small calanoids in the second species pairing (Figures 4 and 5).

Compared to allopatric herring, the utilization of principal prey by herring sympatric with pink salmon was lower, but it was not lower for herring sympatric with sandlance. For herring sympatric with pink salmon, small calanoid number, biomass, percent number, and percent biomass were all lower (P < 0.0321; Table 10a) than values for allopatric herring. The median percent biomass of small calanoids, for example, was 5.2% compared to 65.5% (P = 0.0091). Paired comparisons were not performed on small calanoid selection values because the interaction between species and aggregation type was not significant for this measure (Table 9). However, the median selection of small calanoids among herring sympatric with pink salmon was -38.1 compared to +5.7 for allopatric herring. For the second most important prey, larvaceans, all five measures of utilization were significantly (P < 0.0344) lower for herring sympatric with pink salmon than for allopatric herring (Figures 4, 5 and 8). For example, the median percent number of larvaceans was 0.4% compared to 7.3% (P = 0.0344). Herring sympatric with pink salmon avoided larvaceans compared to allopatric herring (L = -6.4 versus +1.3; Rank Sum Test, P = 0.0030; Figure 8). Herring sympatric with pink salmon also consumed significantly more chaeto-gnaths, large calanoids and hyperiid amphipods (P > 0.0010) than allopatric herring.

For herring sympatric with sandlance, none of the measures of prey utilization were significantly lower than for allopatric herring. Small calanoids comprised similar (P = 0.7549) prey percent biomass, for example, 66.6% for herring sympatric with sandlance and 65.6% for allopatric herring. Median selection value for small calanoids was +0.3 for herring sympatric with sandlance compared to 5.7 for allopatric herring. For larvacean prey, the median percent biomass

consumed in these aggregations was also similar (P = 0.2835), 4.6% and 2.4%, respectively. Larvaceans were selected by allopatric herring and by herring sympatric with sandlance in proportion to their abundance in zooplankton (L = 0.2 vs. +1.3; Rank Sum Test, P = 0.5885).

Pink Salmon

For pink salmon in both types of sympatric aggregations, two of the four total feeding measures were significantly lower (P < 0.05; Table 4; Figure 7) than for allopatric pink salmon. Allopatric pink salmon had the highest fullness index (75%) and prey %BW (1.6%) among these aggregations. Pink salmon sympatric with herring had significantly lower stomach fullness (50%; P = 0.0138) and prey %BW (0.8%; P < 0.0001). However, total prey numbers were not different (P = 0.2550) and prey biomass was slightly greater (P = 0.0371) than comparable measures for allopatric pink salmon. Stomachs of pink salmon sympatric with sandlance were the least full, only 25% (P = 0.0099) and prey %BW was the lowest, only 0.5% (P < 0.0001), of all pink salmon. However, total prey numbers for pink salmon sympatric with sandlance were significantly higher (P = 0.0378) and prey biomass was not different (P = 0.3568) than for allopatric pink salmon.

The overall diet of allopatric pink salmon was similar to the diet of pink salmon sympatric with herring (Table 8). The PSI was greater than 60% by both number and biomass of prey species. The diet of allopatric pink salmon was also similar to the diet of pink salmon sympatric with sandlance, but only when compared as percent number of prey species. The majority of the prey in common was larvaceans and fish (Figures 4 and 5).

Neither category of sympatric pink salmon utilized less of the principal prey, larvaceans, than allopatric pink salmon (P > 0.0587; Table 10b). Larvaceans constituted high median percent numbers (88-97%) and were strongly selected for by pink salmon in all aggregation categories (L > +80; Figure 8). Small calanoids were strongly avoided by all categories of pink salmon (L < -80). No biologically important differences in the consumption of small calanoids were found for pink salmon sympatric with herring (Rank Sum Test, P > 0.0411). Fish were consumed by pink salmon in 7 out of 10 total hauls, but predation was uneven, as shown by the contrast between mean and median utilization values. Pink salmon sympatric with herring had two measures of fish prey utilization that were significantly lower than for allopatric pink salmon (percent number and selection, P < 0.0443), and three measures that were marginally lower (0.05 < P < 0.10). Pink salmon sympatric with sandlance had no measures of any prey category that were significantly different from allopatric pink salmon. For minor prey categories that contributed < 5% to the diets of pink salmon (decapods and hyperiid amphipods), small, but significant (P < 0.05) differences in utilization were observed between allopatric and sympatric aggregations.

Sandlance

Measures of total feeding for sympatric sandlance were significantly less than those of allopatric sandlance only when sandlance co-occurred with herring. Allopatric sandlance

stomachs were 50% full, containing a median of 450 prey items weighing 25.74 mg; prey constituted 0.7% BW (Table 4). For sandlance sympatric with herring, we observed significantly lower medians for stomach fullness (trace%; $P < 0.0001$), prey number (14.5 items; $P = 0.0120$) and prey biomass (0.67 mg; $P = 0.0172$); however, prey %BW was not significantly lower (0.4%; $P = 0.3285$; Figure 7). For sandlance sympatric with pink salmon (a single set), no measures of total feeding were significantly ($P > 0.3560$) different from those of allopatric sandlance.

The overall diet of allopatric sandlance was similar to the diet of sandlance sympatric with herring only when compared as percent biomass of prey species (PSI = 60.5; Table 8). The diet of allopatric sandlance was not similar (PSI < 60%) to the diet of sandlance sympatric with pink salmon either in prey number or biomass. Although sandlance in both aggregation categories did eat small calanoids principally, the taxa differed for the allopatric and sympatric fish (Figures 4 and 5).

Compared to allopatric sandlance, the utilization and selection of principal prey (small calanoids and larvaceans) by sandlance sympatric with herring were lower ($P < 0.0381$; Table 10c). Small calanoids comprised less than 49% of the prey (numbers or biomass) of sandlance sympatric with herring, significantly ($P < 0.0057$; Rank Sum Test) less than the >70% observed for allopatric sandlance. Paired comparisons of small calanoids selection were not performed. Nonetheless, in contrast to allopatric sandlance, sandlance sympatric with herring tended to avoid small calanoids (L = +0.7 vs. -31.4; Figure 8). Larvaceans represented small proportions of sandlance diets (less than 3.2% by number), but significantly lower measures of utilization were observed for sandlance sympatric with herring ($P < 0.0010$) compared to allopatric herring. Larvacean selection values were negative and did not differ significantly ($P = 0.2723$) from those of allopatric sandlance.

For sandlance sympatric with pink salmon, most measures of the utilization and selection of principal prey were not lower than those for allopatric sandlance ($P > 0.0752$). The percent number of small calanoids was greater ($P = 0.0278$) for sandlance sympatric with pink salmon, 94.8% vs. 76.0% for allopatric sandlance. Compared to allopatric sandlance, sandlance sympatric with pink salmon tended to select small calanoids (L = +10.3 vs. +0.7; Figure 8). Larvacean selection values were not different ($P = 0.1340$), both being negative and of similar magnitude. No significant differences were observed in the utilization of minor prey taxa ($P > 0.05$); selection values differed ($P < 0.0332$) but all were near 0.

Discussion - Chapter 3

Few reports exist that examine the co-occurrence and compare the diets of juvenile Pacific herring, Pacific Sandlance, and pink salmon. These species are common residents of nearshore habitats on the Pacific and Arctic coasts in spring and summer (Craig 1984; Cross et al. 1978; Orsi and Landingham 1985; Robards and Piatt 1997; Rogers et al. 1986; Simenstad et al. 1979; Willette et al. in prep.). Their early life history strategies ensure that their spatial and temporal distributions overlap during parts of the juvenile period. Species interactions may be complex, but

sharing of habitat and prey resources among them is to be expected at least some of the time. Generally, in the spring, herring larvae hatch in the intertidal zone and spend the first two years of life nearshore (Norcross et al. 1998). Sandlance larvae also hatch intertidally, disperse, then move onshore later in summer (McGurk and Warburton 1992; Blackburn and Anderson 1997). Pink salmon fry migrate from fresh water to nearshore estuaries in the spring before moving to the Gulf of Alaska in the summer of their first year of life (Heard 1991). Population pulses are especially pronounced in areas where hundreds of millions of salmon are released by hatcheries (Heard 1997). These species' spatial overlaps must decline by fall-winter, when pink salmon have left nearshore waters (Heard 1991), sandlance become dormant in soft substrates (Ciannelli 1997), and older juvenile herring have migrated to deeper water (Norcross et al. 1998).

Ours is not the first study to report mixed schools (sympatry) of these or similar species. Richards (1976) observed sympatric schools of Atlantic herring (*Clupea harengus*) and sandlance (*Ammodytes hexapterus*) juveniles. Sekiguchi et al (1974) reported on the feeding habits of YOY *A. personatus* and anchovy (*Engraulis japonica*) collected in trawls in Japanese waters. Likewise, herring-sandlance and herring-salmon co-occurred near Kodiak, Alaska (Harris and Hartt 1977; Haegele 1996). In July of 1996, up to 11% of our survey net hauls in PWS caught juvenile Pacific herring, Pacific sandlance or pink salmon, with close to half of these catching two of the species. Rates of sympatry are likely to be higher if sympatry is loosely defined, for example as two species caught in consecutive hauls at a sampling station. In our report, feeding of sympatric species refers to mixed species aggregations.

Although we have data only for mid-summer, fish diets can vary with ontogeny, season, habitat and even time of day (e.g.. Simenstad 1979; Sturdevant et. al 1996; Willette et. al in prep; Craig 1987; Gordon 1984). Seasonal changes in abundance and distribution could affect both the potential for food and habitat competition among these species and their availability to marine predators. Willette et al. (in prep) observed monthly changes in the frequency of species associations in the southwestern region of PWS from April to October, 1994. The species associations, as well as frequencies of occurrence and abundance of juvenile herring, pink salmon and sandlance, varied widely over time. In general, herring and pink salmon both co-occurred with sandlance earlier than with each other. Pink salmon and sandlance co-occurred together more often than either did with herring. This information suggests that diet overlap and competition for food are likely to occur for portions of the populations in summer.

A comparison of the size of fish species in different categories of aggregations is important because diet can change with size, because of size-selective predation, and because energy requirements can change with growth. Two species with similar feeding habits may avoid competition by feeding in different areas or by feeding in sympatric aggregations with individuals of a different size that have different prey requirements. Our data suggests that some species associations may be size-related. We observed a wide size range of co-occurring herring and sandlance, but those at a given station were similar in size. The pattern of pink salmon size associations with herring was more variable. Size associations may also reflect seasonal patterns of growth and movement. In our study, most of the larger fish of each species were collected in different habitat than the smaller fish, in water as deep as 36 m with purse seines vs. onshore with beach seines. By late summer, juvenile pink salmon are much less abundant in nearshore waters

than in spring, most having migrated offshore toward the Gulf of Alaska.

The declines in total feeding observed for sympatric fish were apparently not related to fish size. Some of these declines suggest that competitive interactions limit feeding. Sympatric herring fed less than allopatric herring regardless of their size or which species they co-occurred with. It is possible that the degree of decline is related to species-size composition of the aggregation, however. Herring fed the least when they co-occurred with pink salmon. For pink salmon, allopatric fish fed better than either category of sympatric pink salmon even though they were smaller. These small, allopatric pink salmon ate more fish prey than the sympatric pink salmon, contributing to the higher feeding measures. Among sandlance, only the smaller specimens with pink salmon fed as well as the allopatric specimens; the sandlance sympatric with herring were the same size as allopatric sandlance, but feeding declined.

In a study of neritic fish assemblages, juvenile Pacific herring, Pacific Sandlance, and pink salmon were grouped into one functional feeding group, pelagic planktivores (Simenstad et al. 1979). Sandlance and herring were defined as obligate, while pink salmon were considered facultative planktivores. The diets of all were dominated by calanoid copepods, although overlap was not reported (Simenstad et. al 1979). Calanoids are commonly reported as the majority of prey found in the stomachs of Pacific herring (Willette et. al 1997), Pacific sandlance (e.g., Meyer et al 1979; Craig 1987; Field 1988), and pink salmon (e.g., Bailey et. al 1975; Sturdevant et. al 1996). This similarity of principal prey has been noted (Hobson 1986; Field 1988; McGurk and Warburton 1992; Chapter 1, this report), but ours is one of few studies to compare the three species.

We also found that small calanoids were the principal prey of Pacific herring and Pacific sandlance, but not of pink salmon. The principal prey of pink salmon was larvaceans, which was second-most important for herring and one of several less prominent prey categories for sand-lance. Oikopleurans have been reported in juvenile salmon diets (e.g., Healey 1991) and as the nearly-exclusive prey of larval sand-eel, *Ammodytes* spp. (Paffenhofer 1976; Wyatt 1971; Ryland 1964) and occur in the diets of adult fish (C. T. Macer in Ryland 1964) in the North Sea. A changing suite of small calanoids and later, oikopleurans, were prominent in juvenile herring diets throughout the spring (Coyle and Paul 1992). In our study, herring selected small calanoids in close proportion to their abundance, while pink salmon avoided them and were highly selective of larvaceans. For pink salmon, prey biomass was dominated by fish and virtually no copepods were consumed. Differences in feeding between fish caught together in purse seines could reflect feeding in different portions of the water column, as was hypothesized for herring and capelin which partitioned prey between surface and water column in Southeast Alaska (Coyle and Paul 1992).

We considered the possibility that differences in diet between aggregation types were due to fish size differences. Different size classes of a species may select different prey species, sizes or stages within major taxon. Such changes in diet with growth have been reported for numerous fish (e.g., LeBrasseur et. al 1969; Hargreaves and LeBrasseur 1986; Healey 1980, 1991). In fact, our finding of significant diet overlap among herring aggregations containing specimens of different sizes indicates little change in diet with growth for herring up to three years of age.

Small calanoids and larvaceans formed the majority of the prey of large herring sympatric with pink salmon and of small herring that were allopatric or sympatric with sandlance, even though the large fish ate marginally more large prey, large calanoids and hyperiids. We could not clearly associate any of the differences in prey consumed by fish species in different aggregations with fish size. However, the calanoids in poor condition in stomachs could have been different species or stages. Sandlance diets were not similar between aggregation types, but all of the calanoid taxa observed were present across all types of aggregations. Similarly, for pink salmon, we did not find greater predation on fish prey by larger individuals. We observed the opposite, in fact: the smallest pink salmon consumed the most fish and exhibited the highest total feeding measures. These observations reinforce the concept of opportunism and facultative planktivory for juvenile pink salmon (Healey 1991).

In our study, overall diet similarities (PSI) were used to indicate potential competitive interactions. We did not observe many instances of diet similarity (PSI $> 60\%$) between allopatric species or between sympatric species (Table 8). Allopatric herring and allopatric sandlance had similar diets that diverged when they became sympatric. This finding suggests that these species have similar prey requirements and that prey partitioning occurs when they share feeding habitats. Another finding supports this interpretation: within-species, allopatric sandlance diets were not similar to sympatric sandlance diets, indicating that a prey shift occurred when sandlance co-occurred with another species. These results suggest a mechanism sandlance use to avoid competition.

No diet shift was indicated by changes in diet similarity between pink salmon and herring or between pink salmon and sandlance. The diets of these species were just as dissimilar when allopatric as when sympatric. Furthermore, a comparison of diets of allopatric fish to diets of the same species when sympatric revealed patterns of diet fidelity for herring and pink salmon. Allopatric herring diets were similar to sympatric herring diets and allopatric pink salmon diets were similar to sympatric pink salmon diets. Because allopatric sandlance diets were not similar (or marginal, at most) to sympatric sandlance diets, the dissimilarity of herring-sandlance diets when sympatric was due to sandlance diet shift, not herring diet shift. The similarity values we report are lower than they would be if calculated based on major taxon instead of species-size.

Because the composition of herring and sandlance diets was similar based on small calanoids (Figures 4 and 5), and yet diet overlap was low in sympatric aggregations, we examined the prey size spectrum of these predators. Although the predominant prey of both herring and sandlance was small calanoids, the suite of available calanoid species and stages may actually be partitioned . Unfortunately, calanoids were often too mangled or digested to identify consistently. These limitations make it difficult to detect selection at the finest levels, prey species and size. We could not make statistical comparisons, but our data suggests that calanoid copepod prey are partitioned by size and species between sympatric herring and sandlance, decreasing the specific overlap. We have found no other report comparing the diets of these two species, but similar observations have been made for pink salmon and sandlance (LeBrasseur et. al 1969). Scott (1973) also observed that *A. dubius* (15-31 cm) filter fed non-selectively on small prey and selected large prey, although large calanoids were their principal prey.

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Avoidance of predation may be another factor that influences the relative size of co-occurring fish species, and therefore the potential for diet overlap, in late summer. Pink salmon, in particular, become piscivorous with growth (Landingham et al. 1997), and both herring and sandlance have been observed in their stomachs. Most of the fish found in the pink salmon stomachs in our study could not be identified. No herring were identified. However, unidentified fish larvae were found in stomachs of both size classes of pink salmon from the only station where 0-age herring (38 mm FL) co-occurred with them (station 10-1B; Table 2). These herring were probably not large enough to avoid predation by the pink salmon. If so, it would obviously be advantageous for such small herring to avoid sympatry with pink salmon and explains the low frequency of co-occurrence that we observed for these sizes of herring and pink salmon. We did identify sandlance from stomachs of pink salmon that were not caught with sandlance (stations 58-2U and 3-2U) and unidentified fish larvae in a pink salmon at the only station where the two co-occurred (48-1B). These sandlance co-occurring with pink salmon may have been large enough to avoid predation (FL = 64 mm). If so, sympatry would not be detrimental with respect to predation.

The declines in feeding that we observed for sympatric forage fish compared to allopatric forage fish may have explanations other than competitive interactions. Principal among them are the that less food was available in the sympatric areas or that fish densities were greater. Fish could have been attracted to areas of initially high food density which they then cropped down. We have no data to support this idea. However, because we could not show significantly lower total zooplankton densities or lower densities of the predominant taxon (Table 5) in areas with sympatric aggregations compared to areas with allopatric aggregations, we concluded that the feeding declines we observed for sympatric fish (Table 4; Figure 8) were not related to prey availability. The lower density trends we observed (Table 7) could be biologically important, however.

Changes in prey density can greatly affect the success of fish feeding. For example, the food supply available to larval herring during autumn and winter was strongly related to their survival (Campbell and Graham 1991). For fish similar in size to the smaller herring we studied, a doubling of the density of zooplankton maximized larval survival, while halving the density decreased survival by 10-16%. Herring larvae feeding on copepod nauplii did well at densities of about $4*\text{liter}^{-1}$ in one study (Purcell and Grover 1990), but another study found that $5\text{-}12*\text{liter}^{-1}$ was needed for good feeding, survival and growth (Kiorboe et al. 1985 in Purcell and Grover 1990). We observed differences in zooplankton mean density as great as 3x between stations. Small calanoids occurred in densities of approximately $2\text{-}3*\text{liter}^{-1}$, with up to $4*\text{liter}^{-1}$ at allopatric aggregations. These density differences could affect the feeding success of small fish. Densities were low compared to reported spring densities. In early May, densities of zooplankton estimated by the same methodology were $6\text{-}7*\text{liter}^{-1}$ in PWS (Celewycz et. al 1997) and up to $16*\text{liter}^{-1}$ in Southeast Alaska (Sturdevant and Landingham 1993).

The direction of the trend in zooplankton density for areas with sympatric herring aggregations varied depending on the co-occurring species. Mean zooplankton density at allopatric herring aggregations was 40% higher than at herring-sandlance aggregations, but was not higher than at herring-pink salmon aggregations. Yet, herring total feeding declined in both

types of sympatric aggregations. However, herring feeding on small calanoids and larvaceans declined only when they were sympatric with pink salmon and not when they were sympatric with sandlance. This is surprising because pink salmon did not feed on the predominant resource, while sandlance did. However, the large herring sympatric with pink salmon also tended to consume more large calanoids and hyperiids, even though these prey were no more abundant at the sympatric aggregations than at the allopatric aggregations. This suggests that, for herring (like pink salmon), the patchy availability of larger prey is important in the bioenergetics of the growing fish, even though the greatest proportion of the diet continues to come from small prey.

Plankton density was also higher for areas with allopatric pink salmon than for areas with pink salmon sympatric with herring. The decline in total feeding measures for pink salmon sympatric with herring could not have been driven by reduced density of the predominant taxon, which they did not feed on. The larvaceans they did feed on also declined, from approximately 300 to $200*m^{-3}$. But for sympatric pink salmon, utilization and selection of larvaceans did not decline when availability declined. Larvaceans made up more than 88% of prey numbers for pink salmon in all aggregation categories, but fish dominated prey biomass. For pink salmon sympatric with herring, measures of fish prey utilization were lower and measures for hyperiid amphipod utilization were higher than for pink salmon in allopatric aggregations. These pink salmon were not larger than the pink salmon with sandlance, which did not shift prey, but they were larger than the allopatric pink salmon. The herring they co-occurred with were also large and also partially shifted prey. These findings suggest that for pink salmon, feeding declines were due to opportunistic feeding on large prey, such as fish and hyperiids, and were perhaps exacerbated by the competition from large herring which had also begun to require larger prey. Because larval fish were not quantitatively sampled by our zooplankton net, we have no estimate of their relative abundance. The occasional availability of larval fish prey with higher nutritional value may be an important factor in the bioenergetics of juvenile pink salmon during late summer. For herring, however, lack of prey switching when principal prey utilization declined suggests that competitive inhibitions did occur. If a size association between sympatric species exists, larger co-occurring fish that require larger prey may both shift the prey resource for which they compete.

Zooplankton densities were lower in areas with sympatric herring and sandlance than in areas where either species occurred in allopatric aggregations. Because their principal prey is the predominant plankter, these trends suggest that the combined feeding of herring and sandlance may have reduced the resource. This idea is supported by the decline in total feeding for both herring and sandlance in sympatric aggregations compared to those in allopatric aggregations. However, herring sympatric with sandlance did not consume less small calanoids or less larvaceans than allopatric herring. Sandlance sympatric with herring did consume less of these prey and tended to consume more alternative prey.

For the single station of sympatric sandlance and pink salmon, zooplankton density was not lower than in areas of allopatric sandlance but was slightly lower than in areas of allopatric pink salmon. This finding may be related to the fact that pink salmon did not contribute to the cropping of small calanoids and is supported by our finding that plankton density was also higher where pink salmon occurred than where either herring or sandlance occurred. When pink salmon and sandlance were sympatric, sandlance feeding did not decline, but pink salmon feeding did.

Sandlance tended to eat more small calanoids when with pink salmon, while pink salmon tended to eat more larvaceans. Because these two species did not have similar diets, competition for available prey was not a limiting factor.

The juvenile fish in our study may also have prey density requirements, but size of prey is also likely to be important (Parsons and LeBrasseur 1969). Large plankters were rare in our 20 m zooplankton samples. Large copepods were not abundant, in contrast to spring samples from PWS (Celewycz et. al 1997; Cooney 1998). Large calanoids are common prey of juvenile herring, pink salmon and sandlance at some times in some areas (LeBrasseur and Parsons 1969; Bailey et al. 1975; Sturdevant et al. 1996; Willette et al 1997). However, we did not commonly observe large calanoids in fish stomachs. This is notable because in July, at least the pink salmon have grown too large to obtain their daily ration from small calanoids, although they will feed on them (LeBrasseur and Parsons 1969). Bailey et al. (1975) concluded that a maximum of 544 copepod prey daily was sufficient for pink salmon up to 58 mm FL. Our result that sympatric pink salmon fed less well than allopatric pink salmon may not have been due to sympatry but to the appropriateness of the available prey size for the smaller allopatric fish. Parsons and LeBrasseur (1970) noted that both prey density and prey size affected the ability of 90 mm pink salmon to obtain their daily ration. If the energy budget of forage species requires a minimum density of appropriately-sized prey in order for calories consumed to balance calories expended, then synergistic effect of larger size, sympatry and lower prey densities could produce food limitations.

Our pink salmon diets consisted of larvaceans and larval fish at all aggregations. Larvaceans were the numerically dominant prey of pink salmon even though their abundance was far exceeded by small calanoids. We observed up to 570 larvaceans (median) in 98 mm pink salmon (Table 4; Table 10b). Other investigators have suggested that larvaceans are targeted by juvenile salmon because they are highly visible (Bailey et. al 1975). When their mucous houses are intact, they are relatively large, and unlike other gelatinous taxa, their caloric density is similar to copepods (Davis et al. 1997). Combined with a low escape response and high visibility, larvaceans may be a rich alternative prey for fish (Knoechel and Steel-Flynn 1989). This may explain why our pink salmon were highly selective of larvaceans even though they contributed < 10% to zooplankton composition, on the order of $0.5*liter^{-1}$. Larvaceans were not more abundant in areas with allopatric aggregations. The decreased energy expenditure to capture prey with a low escape response could also decrease the rate of encounters with a competitor.

We did not observe shifts in the principal prey targeted by any of the fish species from allopatry to sympatry. However, we did observe shifts in the proportions that the principal prey contributed to the diets. Prey shifts occurred for herring only when they were sympatric with pink salmon, not when they were sympatric with sandlance. Herring consumed proportionately less small calanoids and larvaceans when sympatric with pink salmon. Pink salmon did not shift prey when sympatric with either species. Shifts occurred for sandlance sympatric with both herring and pink salmon. Sandlance shifted away from their principal prey, small calanoids, when with the herring that also ate small calanoids, and increased consumption of small calanoids when with pink salmon, which did not eat small calanoids. Sandlance shifted away from larvaceans and tended to increase prey diversity when sympatric with either herring or pink salmon.

Sandlance were the most adaptable of these species when in sympatric aggregations. Sandlance prey utilization shifted when they were sympatric with either pink salmon or herring, but their total food consumption declined only when they were with herring. Sandlance with pink salmon was the only sympatric species combination in which feeding did not decline significantly from the amount consumed in allopatric aggregations. This was possible because of complete prey partitioning, yet the sandlance were large enough to avoid predation by the pink salmon. However, sandlance mean stomach fullness was already the lowest observed for these species, suggesting a factor other than competition contributed to the low incidence of feeding. Pacific sandlance are known to have a longer digestion time and food retention in the gut (Ciannelli 1997), so perhaps they feed less frequently than other species. The lesser sandeel, *A. marinus*, remained buried longer when food abundances were low (Winslade 1974).

Density dependent interactions could also explain the declines in feeding we observed for sympatric fish. However, because we did not find differences in the ln-transformed catch at allopatric and sympatric stations for any species, we concluded that the declines in total feeding and the prey shifts we observed among species between fish in allopatric and sympatric aggregations were not density-dependent differences. However, these indices of abundance may be very low (see Haldorson et. al 1997). Paul and Willette (1997) concluded that growth of pink salmon may have been limited by intraspecific, density-dependent competition for food in western PWS, and noted a lack of data on the abundance of other competitors. For all of these species, the degree of food-limiting, negative interactions and competition experienced in spring and summer could have a profound effect on nutritional status and survival.

In summary, juvenile Pacific herring, Pacific sandlance and pink salmon co-occur commonly during spring (Willette et al. in prep) and summer in PWS. Forage fish catches were variable but we could not attribute feeding declines to density dependent interactions. Diets of herring and sandlance were sometimes similar, but pink salmon consumed different prey. All, however, exhibited reduced feeding when sympatric. The declines may have been related to reduced prey densities in some cases. Contrary to others' findings of a specialized diet for sandlance (Simenstad et al. 1979) we found that sandlance were the more adaptive of these species because of their feeding flexibility. Our findings suggest that pink salmon and herring had distinctive diets which they adhered to even when sympatric with another species. Sandlance adhered less strongly to the preferred diet when sympatric.

Our findings from tests of diet similarity indicate several important ideas about the trophic relationships of these species: 1) that herring and sandlance consume similar prey when in allopatric aggregations, but when co-occurring in the same prey environment, they tend to partition prey; 2) sandlance shifted prey most; and 3) pink salmon and herring adhere to similar diets whether allopatric or sympatric. Diet shifts were generally not disadvantageous in terms of nutritional value. The predominantly crustacean prey, as well as larvaceans, are all relatively energy dense (Davis et. al 1996). However, total food consumption decreased for all three species when they were sympatric compared to when they were allopatric. This downward shift in feeding, which occurred even though lower plankton densities in areas of some sympatric aggregations were not significant and composition did not differ between allopatric and sympatric stations, suggests that competitive interactions do occur among nearshore forage species. The

behavioral interactions which reduce feeding or cause prey shifts in these forage species have not been examined. The lack of differences in zooplankton and the overabundance of available small calanoids suggested by negative selection values for them indicate that reduced availability of prey was not the principal cause of feeding declines. Rather, fish interactions that inhibit feeding, such as aggressive behavior, could result in the observed feeding declines. This would also explain our observations of reduced feeding even when two species do not prey on the same taxa. Pink salmon and sandlance, for instance, did not compete for the same foods, yet both fed less in the presence of the other. The intensity/frequency of these interactions and their negative effects could vary with shifts in the component species densities/abundances between years and areas. Competition resulting in a less ideal diet, either in composition or quantity, could lead to lower survival or slower growth. Such effects of competitive interactions among forage fish remain to be tested, but if forage species occur sympatrically frequently enough to suggest that competition is a regulating factor, their interactions could lead to a decrease in the availability of high quality forage species to marine birds and mammals.

Acknowledgments - Chapter 3

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